

## Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage

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Field metabolic rates (FMR) and activity patterns of black-browed albatrosses *Thalassarche melanophrys* were measured while at sea and on nest during the incubation stage at Kerguelen Island, southwestern Indian Ocean. Activity-specific metabolic rates of five albatrosses at sea ( $FMR_{\text{at-sea}}$ ) were measured using doubly labeled water (DLW), and by equipping birds with wet-dry activity data loggers that determined when birds were in flight or on the water. The metabolic rates of four birds incubating their eggs ( $FMR_{\text{on-nest}}$ ) were also measured using DLW. The mean  $\pm$  SD  $FMR_{\text{at-sea}}$  of albatrosses was  $611 \pm 96 \text{ kJ kg}^{-1} \text{ d}^{-1}$  compared to  $FMR_{\text{on-nest}}$  of  $196 \pm 52 \text{ kJ kg}^{-1} \text{ d}^{-1}$ . While at sea, albatrosses spent  $52.9 \pm 8.2\%$  ( $N = 3$ ) of their time in flight and they landed on the water  $41.2 \pm 13.9$  times per day. The FMR of black-browed albatrosses appear to be intermediate to that of three other albatross species. Based on at-sea activity, the power requirement of flight was estimated to be  $8.7 \text{ W kg}^{-1}$  (or  $4.0 \times$  predicted BMR), which is high compared to other albatross species, but may be explained by the high activity levels of the birds when at sea. The  $FMR_{\text{at-sea}}$  of albatrosses, when scaled with body mass, are lower than other seabirds of similar body size, which probably reflects the economical nature of their soaring flight.

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Our ability to measure energetic costs associated with daily activities during reproduction can provide valuable insight into ecological comparisons of animal populations within or between species, or of higher taxonomic levels (Nagy et al. 1984, Costa and Prince 1987, Chappell et al. 1993, Nagy et al. 1999). Furthermore, patterns of energy output may be useful for describing differences in life history strategies of animals because energy usage and allocation vary with reproductive effort (Goodman 1974, Stearns 1992).

For birds, the energetic costs associated with reproduction can generally be broken down into discrete stages: egg incubation and chick-rearing. Without question, there is ample evidence, which shows that the chick-rearing stage places a significant energy demand on

parents (Drent and Daan 1980, Chappell et al. 1993, Daan et al. 1996, Shaffer et al. 2003). However, the incubation stage can also entail a substantial drain on the energy reserves of adults, particularly when parents brood a large clutch of eggs or undergo prolonged fasting during a bout on the nest (see reviews Williams 1996, Thomson et al. 1998, Tinbergen and Williams 2002). This latter point is especially prevalent in many seabird species because resources are often distributed at considerable distances from the breeding colony (Ashmole 1971), so both partners of a brood must alternate between incubating the clutch and foraging at sea (Lack 1968). Since parents are not provisioning chicks during the incubation stage, foraging effort is mainly predicated on the restoration of energy reserves

that were used during the preceding shift on the nest (Ricklefs 1983, Shaffer et al. 2003). Given that some species undergo prolonged excursions at sea during this phase (e.g. many albatrosses, petrels, and penguins), the partner that is left to incubate the brood may experience significant energy shortages after fasting for days, weeks, or longer. Thus, energy demands during incubation can be an important, but often undervalued, component of reproduction and life history in birds (Thomson et al. 1998, Tinbergen and Williams 2002).

In order to evaluate the overall energy output of parents during the incubation phase, it is important to measure the cost and activity of adults both on and away from the nest. In many cases, it is not possible to observe parents when they forage away from the nest. However, the use of archival data loggers in combination with methods to measure energy expenditure permit investigators to evaluate the cost of specific activities like foraging (Arnould et al. 1996, Weimerskirch et al. 2000), flight (Bevan et al. 1995, Shaffer et al. 2001a), or swimming and diving (Nagy et al. 1984, Chappell et al. 1993). In contrast, measurements of energy expenditure and activity of adults at the nest are easier to obtain, especially for species that nest in the open (e.g. colonial nesting seabirds), because adults are tied to the nest to protect and incubate their eggs (Lack 1968, Ricklefs 1983, Warham 1990).

Procellariiform seabirds (albatrosses and petrels) are particularly good subjects to study the patterns of energy output during the incubation stage because they lay only a single egg (Lack 1968, Ricklefs 1990), so brood size is fixed. Furthermore, albatrosses in particular nest in open areas in dense colonies so observation and access to nesting birds can be ideal. Finally, there have been in recent years a number of studies that have measured energy output in albatrosses, so it is now possible to evaluate the allometric relationships between albatrosses and other bird species to examine fundamental differences in metabolic expenditure during reproduction. Thus, the objective of our study was to measure activity-specific metabolic rates of black-browed albatrosses *Thalassarche melanophrys* while at sea ( $FMR_{at-sea}$ ) and on the nest ( $FMR_{on-nest}$ ) during the incubation stage of reproduction. Activity patterns of albatrosses at sea were studied by equipping birds with data loggers that allowed us to delineate when birds were in flight or on the water, thus permitting us to estimate the cost of flight. Also, we compared the metabolic costs of black-browed albatrosses at sea, on nest, and a combined average for the incubation cycle, to those of other albatross species. Lastly, allometric relationships of several seabird orders were compared to evaluate the  $FMR_{at-sea}$  during reproduction.

## Materials and methods

Black-browed albatrosses were studied during the incubation period of Nov-Dec 1999 on Kerguelen Island, southwestern Indian Ocean (50°S, 70°E). At this time, albatrosses were at or near the mid-point of their incubation cycle, which lasts about 68 days (Tickell and Pinder 1975). The breeding colony is located at Cañon des Sourcils Noirs, Jeanne d'Arc Peninsula in the southeast sector of the Island. This breeding colony has ca. 1,200 breeding pairs of black-browed albatrosses, but seven study nests were monitored from a vantage point on a cliff above the colony. To distinguish between individuals in a pair, one adult from each nest was marked on the breast with a yellow patch of picric acid, which could easily be seen with binoculars.

Field metabolic rates (FMR) and total water influx rates (TWI) of albatrosses at sea and on the nest were measured using the doubly labeled water (DLW) method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980, Speakman 1997). Details of the methods used in this study can be found in Shaffer et al. (2001a, b, 2003). However, in brief, albatrosses departing to sea were captured near their nests whereas birds just beginning an incubation shift were removed from their nest and their eggs were covered with a cloth. A background blood sample was collected from an intertarsal vein, and then birds were injected (intra-peritoneal) with sterile DLW containing 10 atom% oxygen-18, 2.23 MBq mL<sup>-1</sup> of tritiated water, and 0.9% NaCl. Albatrosses heading to sea were given 8–9 mL of DLW and birds at the nest were given 4 mL of DLW. The masses of injected volumes were determined gravimetrically with a portable field balance ( $\pm 0.01$  g). All birds were placed into a cloth sack and weighed ( $\pm 50$  g) using a spring balance scale (Pesola, Model 80005, Baar, Switzerland). Isotopes were allowed to equilibrate with total body water for approximately 90 min (Degen et al. 1981, Shaffer et al. 2001b) and then another blood sample was collected. Birds were then released near their nests and allowed to depart or to continue incubating their eggs. After returning from sea, or after 2–3 days of a bout on the nest, injected birds were recaptured, a final blood sample was collected and final body mass was measured.

Blood samples were centrifuged for 10 min at 1000 g, then serum was transferred to plastic screw cap vials and frozen at  $-5^{\circ}\text{C}$  until analyses were performed 6 months later. Specific activity of tritiated body water was determined in triplicate by scintillation spectrometry (Beckman LS 6500, Beckman Coulter Inc., Fullerton, CA, USA) of water obtained from serum using the freeze-trap method (Ortiz et al. 1978). Specific activity of oxygen-18 water was determined by mass ratio spectrometry of water distilled from serum (Metabolic Solutions, Nashua, NH, USA).

The initial dilution space of oxygen-18 was used to calculate initial total body water (TBW) content in mL, and final body water content was calculated as the initial fractional water content multiplied by final body mass. CO<sub>2</sub> production was calculated using equation 2 in Nagy (1980), and TWI was calculated using equations 4 and 6 in Nagy and Costa (1980). CO<sub>2</sub> production (in mL g<sup>-1</sup> hr<sup>-1</sup>) was converted to FMR (kJ d<sup>-1</sup>) using a conversion factor of 1 liter CO<sub>2</sub> = 26.2 kJ, which was derived for black-browed albatrosses based a diet of 31% squid, 30% fish, and 39% krill (Reid et al. 1996). The compositional make up and energy content of this diet was obtained from Clarke and Prince (1980) and conversion of fat, protein, and carbohydrates into CO<sub>2</sub> was derived from factors given in Schmidt-Nielsen (1990).

In two cases (birds 3w and 6w), FMR<sub>at-sea</sub> was measured before FMR<sub>on-nest</sub> in the same individual. Both birds were weighed and final blood samples were collected upon returning from sea and then again after a bout on the nest. To calculate FMR<sub>on-nest</sub>, initial fractional TBW (i.e. % of mass) was assumed to remain constant between sampling periods. This was done in lieu of re-evaluating TBW at the beginning of the bout on the nest because we did not want to risk nest abandonment from the manipulation. Furthermore, the variation in fractional TBW for all birds combined was low (52.5 ± 3.3% of mass) and not statistically different between birds (Kruskal-Wallis ANOVA, U = 14, P = 0.32) that went to sea vs. those that were studied at the nest. A similar result has also been observed in wandering albatrosses *Diomedea exulans* using the same methodology (Shaffer et al. 2001b).

The duration at sea was determined by direct observation of departure and return times, and/or by the analysis of activity logger data (described below). Because DLW measurement intervals included brief periods ashore before and after birds returned from sea, FMR<sub>at-sea</sub> was corrected following methods of Costa and Prince (1987) and Shaffer et al. (2001a).

Activity patterns of birds at sea were studied using 12 g Wet-Dry activity data loggers (Francis Scientific Instruments, Cambridge, UK) taped to a plastic darvic band that was placed around a birds' tarsus. The loggers were programmed to sample whether the device was wet or dry every 5 seconds, indicating that a bird was either in flight (logger dry) or on the water (logger wet). Electrical contacts on the loggers were located at opposite ends, so the device had to be submerged in water for the contacts to indicate a wet condition. Thus, it was not possible for raindrops or sea spray to incorrectly cause the logger to record a wet event. Because the time of day for each landing and take-off was determined, we quantified both the daily and total activity budget of each albatross in combination with measuring FMR<sub>at-sea</sub>. Day length was based on calcula-

tions of sunrise and sunset for the region around Kerguelen Islands, assuming all birds foraged along the Kerguelen shelfbreak waters. This assumption is valid because two studies conducted at the same breeding colony (Weimerskirch et al. 1997, Pinaud and Weimerskirch 2002) showed that nearly all black-browed albatrosses from this colony commute directly between the shelf edge along the Kerguelen Plateau and the breeding colony.

Statistical analyses were performed using Systat 10 (SPSS Inc, Chicago, IL, USA) with a significance level of P ≤ 0.05 for t-tests, ANCOVA, and non-parametric statistics where appropriate. All data presented are means ± 1 standard deviation (SD).

## Results

Average daily mass change of albatrosses at sea was 31 g d<sup>-1</sup>, or a gain of 0.8% of body mass per day over a mean duration of 4.14 ± 1.24 days. On the nest, albatrosses lost an average of 96 g d<sup>-1</sup>, or about 2.4% of body mass per day while sitting on the nest for 2.19 ± 0.34 days (Table 1). Initial TBW (% of mass) was not significantly different (U = 14, N = 9, P = 0.32) between birds heading to sea vs. those just starting a bout on the nest.

Mean energy expenditure of albatrosses at sea (2,352 ± 335 kJ d<sup>-1</sup>) was 3 times greater than that of birds on the nest (786 ± 238 kJ d<sup>-1</sup>; U = 20, N = 9, P = 0.01). Similarly, mean TWI was 8 times greater and significantly more variable (F-test for equality of variances, F = 176, P < 0.01) for birds at sea than that of birds on the nest (Table 1; U = 20, N = 9, P = 0.01). TBW turnover of albatrosses at sea was approximately 22% per day compared to a turnover of 3% per day in albatrosses on the nest.

At-sea activity levels were only measured for 3 albatrosses because one data logger malfunctioned on the deployment and another bird was not equipped with a data logger (see Table 1 for details). Nevertheless, there was a general pattern for 3 of the albatrosses to make only a few landings and take-offs of short duration (< 10 min) during the first 4–5 hours after leaving the colony. This pattern was repeated on the return trip back to the colony. On average, albatrosses spent 52.9 ± 8.2% per day in flight over the entire trip to sea. During daylight hours, mean time in flight between consecutive landings and take-offs was 35.0 ± 8.8 min and the mean time on water between consecutive flights was 16.1 ± 6.8 min. At night, albatrosses spent on average 31.2 ± 13.4 min in flight between consecutive landings and take-offs, and 46.2 ± 11.6 min on the water between consecutive flights. Mean number of landings and take-offs per day was 41.2 ± 13.9 and the majority were during daylight hours (Table 1). Even though albatrosses landed on the surface more during the day than at night, a mean of 75.1 ± 2.0%

Table 1. Summary statistics of study duration, mass change, field metabolic rate, and activity of black-browed albatrosses during the incubation stage in 1999.

Bird	Study period	DLW interval(d)	Time in activity (d)	Initial mass (kg)	Total mass change (kg)	Daily mass change (g d <sup>-1</sup> )	TBW <sub>i</sub> (% of mass)	CO <sub>2</sub> prod.	FMR	TWI	Time in flight (%)	Landings per trip	Landings in daylight hours
<b>At sea</b>													
3w	20–25 Nov	5.21	5.08	3.58	+0.63	+121	55.8	1.079	2691	693	*	*	*
6w	24–28 Nov	4.00	3.13	4.22	-0.02	-5	47.9	0.786	2430	366	51.9	146	97
7y	26–30 Nov	3.90	3.24	3.81	+0.14	+36	56.5	0.917	2538	361	61.5	82	59
11y	1–7 Dec	5.98	5.85	3.28	+0.22	+37	54.1	1.057	2288	509	45.2	297	204
13y	2–7 Dec	5.08	3.40	4.05	-0.17	-34	52.2	0.590	1814	282	**	**	**
	Mean	4.83	4.14	3.79	+0.16	+31	53.3	0.886	2352	442	52.9	175.0	120.0
	SD	0.88	1.24	0.37	0.30	58	3.4	0.203	335	162	8.2	110.4	75.2
<b>On nest</b>													
3w	25–28 Nov	2.70	2.70	4.21	-0.36	-133	55.8	0.289	732	59	-	-	-
6w	28–30 Nov	2.04	2.04	4.20	-0.19	-93	47.9	0.385	994	38	-	-	-
8w	26–28 Nov	2.01	2.01	4.15	-0.15	-75	50.4	0.369	946	67	-	-	-
15y	3–5 Dec	2.02	2.02	3.74	-0.17	-84	52.0	0.206	473	56	-	-	-
	Mean	2.19	2.19	4.08	-0.22	-96	51.5	0.312	786	55	-	-	-
	SD	0.34	0.34	0.23	0.10	26	3.3	0.082	238	12	-	-	-

TBW<sub>i</sub> – Initial total body water determined from the dilution of oxygen-18 in total body water.

CO<sub>2</sub> prod. – CO<sub>2</sub> production in mL g<sup>-1</sup> hr<sup>-1</sup> calculated from equation 2 in Nagy (1980).

FMR – Field metabolic rate in kJ day<sup>-1</sup> using a conversion factor of 1 liter CO<sub>2</sub> = 26.2 kJ.

TWI – Total Water Influx rate in mL d<sup>-1</sup> calculated from equation 4 & 6 in Nagy and Costa (1980).

\* – Not equipped with an activity recorder.

\*\* – No data were obtained because activity recorder malfunctioned.

of daylight hours were spent in flight compared to a mean of only  $38.2 \pm 18.1\%$  of nighttime hours spent in flight.

## Discussion

The results of our study show that black-browed albatrosses use  $611 \text{ kJ kg}^{-1} \text{ d}^{-1}$  while at sea,  $196 \text{ kJ kg}^{-1} \text{ d}^{-1}$  while on the nest, and a combined average expenditure of  $427 \text{ kJ kg}^{-1} \text{ d}^{-1}$  during the incubation stage. The level of energy output in black-browed albatrosses while on the nest is similar to Laysan *Phoebastria immutabilis*, shy *Thalassarche cauta*, and wandering albatrosses (Fig. 1). However, at-sea energy expenditure is more variable between species, with a substantially lower  $\text{FMR}_{\text{at-sea}}$  in wandering albatrosses. The difference in FMR between species is at least partially influenced by variations in body mass because black-browed, Laysan, and shy albatrosses are considerably smaller 3–4 kg (Pettit et al. 1988, Green and Brothers 1995, this study) than wandering albatrosses, which average 8–10 kg (Tickell 1968). Another difference is probably related to at-sea activity patterns because black-browed and Laysan albatrosses exhibit higher activity levels (e.g. more landings and take-offs) compared to wandering albatrosses (see below; Fernández and Anderson 2000, Weimerskirch and Guionnet 2002). It is also interesting to note that despite having similar  $\text{FMR}_{\text{on-nest}}$ , conditions at the breeding

locations where the four albatross species breed varies from sub-tropical (Laysan albatrosses) to sub-Antarctic (other albatross species).

## Energy expenditure of black-browed albatrosses

This study was the first to measure field metabolic rates of free-ranging black-browed albatrosses at sea and on nest using doubly labeled water (DLW). However, energy expenditures of black-browed albatrosses have been measured using other techniques. For example, Bevan et al. (1995) used heart rate as a proxy for oxygen consumption and estimated that at-sea cost was  $408 \text{ kJ kg}^{-1} \text{ d}^{-1}$  whereas on-nest cost was  $192 \text{ kJ kg}^{-1} \text{ d}^{-1}$ . Although cost on nest was nearly identical to our estimate, at-sea cost estimated by the heart rate method was 33% lower than our estimate using DLW. It is unclear why such a large discrepancy exists between estimates for black-browed albatrosses at sea and not for birds on the nest. However, recent evidence suggests that the heart rate method can significantly underestimate the cost of flight if calibration between heart rate and oxygen consumption is not performed on birds engaged in flight (Ward et al. 2002). Bevan et al. (1995) calibrated their method by walking albatrosses on a treadmill to increase the energy output to match that, which would be expected to occur during activity at sea. In light of the conclusions of Ward et al. (2002), it is unclear how the differences in calibration methods could have affected estimates of energy expenditure in black-browed albatrosses. Certainly, more validation/calibration of this technique, by studying birds in flight, should be performed to fully evaluate the accuracy of energy expenditure estimates from heart rate in albatrosses at sea.

It is also conceivable that DLW overestimated FMR of black-browed albatrosses at sea, which could have resulted from 1) physical fractionation of the isotopes, and/or 2) uptake of isotopes into non-aqueous tissues such as lipids (Nagy 1980, Speakman 1997). These errors can lead to substantial variation in the results of individual animals (Bevan et al. 1994). However, mean algebraic error of estimates in  $\text{CO}_2$  production validated against respirometry or energy balance method is generally within 10% (Nagy 1980, Bevan et al. 1994, Speakman 1997). Nevertheless more validation studies are required, particularly those which utilize several techniques simultaneously to measure energy expenditure on the same individual.

Another plausible explanation for the difference in  $\text{FMR}_{\text{at-sea}}$  between our study and that of Bevan et al. (1995) could be related to activity levels of the study birds. However, Bevan et al. (1995) were not able to quantify the number the landings and take-offs due to the time resolution of their activity recorders, so direct comparison of activity patterns with our data is not

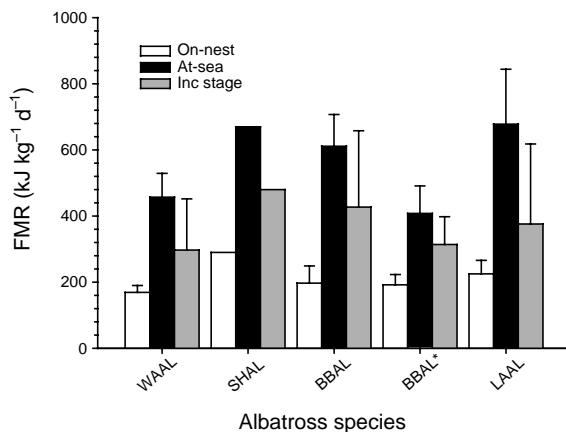


Fig. 1. Field metabolic rates of albatrosses at sea, on nest, and a combined average of both during the incubation stage. All measurements were obtained using doubly labeled water except those of BBAL\*, which were estimated using measures of heart rate (Bevan et al. 1995). Species names and sources of data are as follows: WAAL – wandering albatross, *Diomedea exulans* (Shaffer et al. 2001a, b); SHAL – shy albatross, *Thalassarche cauta* (Green and Brothers 1995); BBAL – black-browed albatross, *T. melanophrys* (this study); LAAL – Laysan albatross, *Phoebastria immutabilis* (Pettit et al. 1988). All values are means  $\pm$  SD, but no variation was reported by the original source for SHAL.

possible. Furthermore, they equipped birds with activity recorders during the brooding stage and previous research shows that foraging effort and activity levels differ between the incubation and chick-brooding stages (Shaffer et al. 2003).

### Activity patterns and flight costs of black-browed albatrosses

The activity patterns of black-browed albatrosses in this study are similar to observations of the same species breeding at the same colony on Kerguelen (Weimerskirch et al. 1997, Pinaud and Weimerskirch 2002), as well as those of birds from other breeding colonies around the Southern Ocean (see Prince and Morgan 1987, Grémillet et al. 2000, Huin 2002, Weimerskirch and Guionnet 2002). However, to evaluate whether our manipulations had an effect on the performance of the birds, we compared the behavior of our study birds with those of another study conducted at the same time (Pinaud and Weimerskirch 2002). On average, the foraging durations of birds in our study ( $4.14 \pm 1.24$  days,  $N=5$ ) were nearly identical to those ( $4.3 \pm 1.4$  days,  $N=40$  pairs) reported in Pinaud and Weimerskirch (2002). Interestingly, time at sea (and duration of shifts on the nest) of black-browed albatrosses breeding at Kerguelen are considerably shorter than those reported for the same species breeding at South Georgia (9–12 days; Tickell and Pinder 1975). One major difference in foraging behavior between breeding colonies is the relative consistency from year to year of Kerguelen birds to forage in the same locations only 200–300 km from the island compared to birds at South Georgia, which frequently travel 1000 km or more to forage (Pinaud and Weimerskirch 2002). Another metric with which to compare to other studies, is the mass change of our study birds. Both the mass gain and loss of birds in our study (Table 1) were within the range of those reported elsewhere (Tickell and Pinder 1975, Pinaud and Weimerskirch 2002). Thus, we are confident that our manipulations in this study had a minimal, if any, effect on the energy expenditures and performance of black-browed albatrosses at sea and on the nest.

Because we are able to differentiate at-sea activity patterns (i.e. in flight vs. on water) of black-browed albatrosses, it is possible to estimate the power required for flight (in watts, W) by combining measurements of energy expenditure and foraging activity. On average, albatrosses spent 53% of each day engaged in flight, so the remainder (47%) is spent sitting on the sea surface, which costs 20.7 W (Bevan et al. 1995). Therefore, the cost of sitting on the sea surface for 11.3 hours would be 9.7 W ( $=20.7 \text{ W} \times 47\%$ ). The integrated power of black-browed albatrosses at sea is 27.2 W (from Table 1), so the cost of flight for 12.7 hours would be 17.5 W ( $=27.2 \text{ W}$

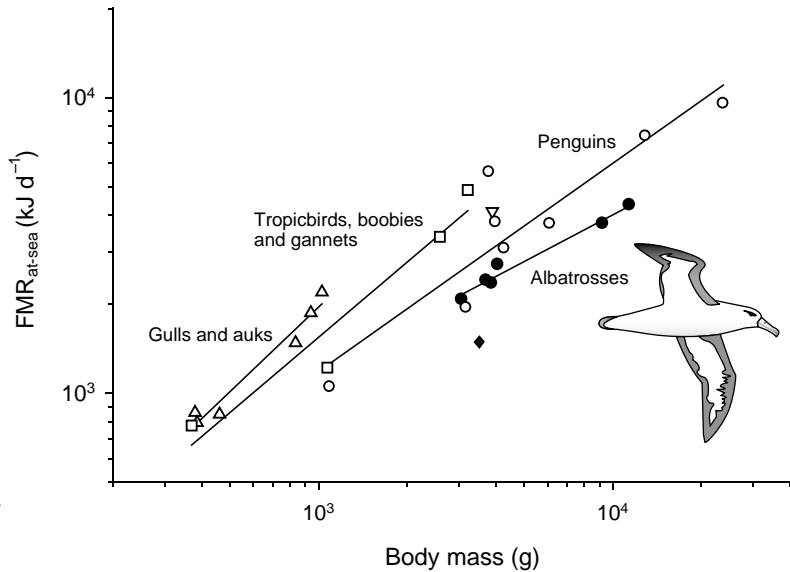
$- 9.7 \text{ W}$ ) or 33.0 W ( $=17.5 \text{ W}/53\%$ ) for 24 hours. This absolute cost of flight is similar to that of 28.7 W estimated for grey-headed albatrosses *T. chrysostoma* (mass 3.71 kg) originally determined by Costa and Prince (1987) and further revised by Bevan et al. (1995), and almost 1.5  $\times$  the estimated power derived from measurements of heart rate for black-browed albatrosses (Bevan et al. 1995). On a relative scale, the cost of flight is 4.0  $\times$  predicted BMR (Ellis and Gabrielsen 2001), which is high compared to other albatross species (2 to 3.2  $\times$  BMR) but still low compared to other seabirds (Shaffer et al. 2001a). One reason flight costs may be higher for black-browed albatrosses compared to other albatross species is the difference in at-sea activity. For example, albatrosses in our study landed and took-off from the sea surface an average of 41 times per day, which is more than twice the activity level of wandering albatrosses that have an estimated flight cost of 2  $\times$  measured BMR (Shaffer et al. 2001a). Taking off and landing on the sea surface requires the use of flapping flight, which has been shown to be energetically expensive for albatrosses (Weimerskirch et al. 2000, Shaffer et al. 2001a). Therefore, the higher cost of flight in black-browed albatrosses may be related to the more frequent use of flapping flight (i.e. more landings and take-offs).

### Allometry and field metabolic rates

With the additional data on FMR in black-browed albatrosses obtained in this study, it is possible to evaluate allometric equations to predict FMR in albatrosses. Croxall (1982) derived an equation to predict the on-nest cost in petrels, albatrosses, and penguins in relation to body mass. The energetic costs were based on the measured rate of mass loss assuming metabolism was proportional to compositional changes in stored fat and protein (Croxall 1982). Equation b in Croxall (1982), predicts a cost of 618 kJ d<sup>-1</sup> for a bird of mass of 3.85 kg, which is 20% lower than measured  $\text{FMR}_{\text{on-nest}}$  of black-browed albatrosses (Table 1) and 8.5% lower than predicted BMR (Ellis and Gabrielsen 2001). In fact, the same equation consistently *underestimated*  $\text{FMR}_{\text{on-nest}}$  for the other albatross species in Fig. 1 (as much as 80% for shy albatross). In a study where  $\text{FMR}_{\text{on-nest}}$  (using DLW) and mass loss were measured simultaneously on the same individuals (Shaffer et al. 2001b), mass loss consistently *overestimated* metabolic rate. Thus caution should be exercised when trying to predict metabolic rate from relationships involving changes in mass loss only.

The relationship between  $\text{FMR}_{\text{at-sea}}$  and body mass in albatrosses had not been adequately established previously because few measurements were available for comparison. However, if we combine our data on black-browed albatrosses and further separate the data for

Fig. 2. Allometry of field metabolic rate ( $FMR_{at-sea}$ ) in albatrosses (●), a giant petrel (v), penguins (○), gulls and auks (Δ), and tropicbirds, boobies and gannets (□).  $FMR_{at-sea}$  of black-browed albatrosses measured using heart rate (Bevan et al. 1995) is given as (◆) and was not included in the regression for the other albatrosses because  $FMR_{at-sea}$  was measured using doubly labeled water. The relationships for all species combine data from studies conducted during all stages of the breeding cycle. The regression statistics and raw data for all relationships except that of the albatrosses can be found in review papers by Nagy et al. (1999), Ellis and Gabrielsen (2001), and the original sources listed therein. The regression for albatrosses was  $FMR = 33.4 \text{ Mass}^{0.519}$  ( $r^2 = 0.967$ ,  $P < 0.01$ , 95% CI of intercept was 10.6–105.2 and 95% CI for the slope was 0.386–0.653).  $FMR$  of all birds (except ◆) was measured using doubly labeled water.



male and female wandering albatrosses since they are sexually size dimorphic (Tickell 1968), energy expenditure at sea scales with body mass in albatrosses as  $FMR_{at-sea} = 33.4 \text{ Mass}^{0.519}$  (Fig. 2;  $r^2 = 0.967$ ,  $N = 6$ ,  $P < 0.01$ ) where  $FMR_{at-sea}$  is in  $\text{kJ d}^{-1}$  and Mass is in grams. To evaluate the predictive power of the equation, we estimate the  $FMR_{at-sea}$  of a 3.86 kg black-browed albatross to be  $2,428 \text{ kJ d}^{-1}$ , which is only 3.2% greater than the measured  $FMR$  (Table 1) and well within the accuracy of estimates obtained using the doubly labeled water method (Nagy 1980, Speakman 1997). Therefore, we are confident that the equation can predict  $FMR_{at-sea}$  of free-ranging albatrosses with reasonable accuracy.

The slope of the equation for albatrosses compared to the slopes of equations for other seabird species appears to be shallower (Fig. 2). However, statistical comparisons of the regressions (i.e. ANCOVA) reveal that no significant difference exists between taxonomic groups, which is consistent with previous analyses (Nagy et al. 1999, Ellis and Gabrielsen 2001). Nevertheless, if we compare seabirds of similar body mass range to the albatrosses, it appears that albatrosses have lower  $FMR_{at-sea}$  than several penguin, gannet, and giant petrel species (Fig. 2). This result is perhaps not all that surprising because albatrosses are specialists at soaring flight (Pennycuik 1982). Thus, a combination of high aspect ratio wings (i.e. long and narrow) and anatomical wing lock mechanism (Pennycuik 1982) permit albatrosses to use prevailing winds to travel rapidly over the sea surface with a minimal amount of energy expenditure (Costa and Prince 1987, Bevan et al. 1995, Weimerskirch et al. 2000, Shaffer et al. 2001a). Undoubtedly, this evolutionary adaptation is likely one of the primary reasons for the success of albatrosses as pelagic foragers in waters that range from the tropics to polar seas.

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## References

- Arnould, J. P. Y., Briggs, D. R., Croxall, J. P., Prince, P. A. and Wood, A. G. 1996. The foraging behaviour and energetics of wandering albatrosses brooding chicks. – *Ant. Sci.* 8: 229–236.
- Ashmole, N. P. 1971. Seabird ecology and the marine environment. – In: Farner, D. S. and King, J. R. (eds). *Avian Biology*. Vol. 1. Academic Press, New York, pp. 223–286.
- Bevan, R. M., Butler, P. J., Woakes, A. J. and Prince, P. A. 1995. The energy expenditure of free-ranging black-browed albatrosses. – *Phil. Trans. R. Soc. Lond. B* 350: 119–131.
- Bevan, R. M., Woakes, A. J., Butler, P. J. and Boyd, I. L. 1994. The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*. – *J. Exp. Biol.* 193: 119–137.
- Chappell, M. A., Shoemaker, V. H., Janes, D. N., Maloney, S. K. and Bucher, T. L. 1993. Energetics of foraging in breeding Adelle penguins. – *Ecology* 74: 2450–2461.
- Clarke, A. and Prince, P. A. 1980. Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. – *Ibis* 122: 488–494.
- Costa, D. P. and Prince, P. A. 1987. Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. – *Ibis* 129: 149–158.

- Croxall, J. P. 1982. Energy costs of incubation and moult in petrels and penguins. – *J. Anim. Ecol.* 51: 177–194.
- Daan, S., Deerenberg, C. and Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. – *J. Anim. Ecol.* 65: 539–544.
- Degen, A. A., Pinshow, B., Alkon, P. U. and Arnon, H. 1981. Tritiated water for estimating total body water and water turnover rate in birds. – *J. Appl. Physiol.* 51: 1183–1188.
- Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. – *Ardea* 68: 225–252.
- Ellis, H. I. and Gabrielsen, G. W. 2001. Energetics of free-ranging seabirds. – In: Schreiber, E. A. and Burger, J. (eds). *Biology of Marine Birds*. CRC Press, Boca Raton, pp. 359–408.
- Fernández, P. and Anderson, D. J. 2000. Nocturnal and diurnal foraging activity of Hawaiian albatrosses detected with a new immersion monitor. – *Condor* 102: 577–584.
- Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. – *Am. Nat.* 108: 247–268.
- Green, B. and Brothers, N. 1995. Field energetics of white-capped albatross *Diomedea cauta cauta* and growth of chicks. – Abstracts of the First International Conference on the Biology and Conservation of Albatrosses, Hobart, Tasmania.
- Grémillet, D., Wilson, R. P., Wanless, S. and Chater, T. 2000. Black-browed albatrosses, international fisheries and the Patagonian Shelf. – *Mar. Ecol. Prog. Ser.* 195: 269–280.
- Huin, N. 2002. Foraging distribution of the black-browed albatross, *Thalassarche melanophris*, breeding in the Falkland Islands. – *Aquatic Conserv. Mar. Freshw. Ecosyst.* 12: 89–99.
- Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen & Co. Ltd, London.
- Lifson, N. and McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. – *J. Theor. Biol.* 12: 46–74.
- Nagy, K. A. 1980. CO<sub>2</sub> production in animals: analysis of potential errors in the doubly labeled water method. – *Am. J. Physiol.* 238: R466–R473.
- Nagy, K. A. and Costa, D. P. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. – *Am. J. Physiol.* 238: R454–R465.
- Nagy, K. A., Girard, I. A. and Brown, T. K. 1999. Energetics of free-ranging mammals, reptiles, and birds. – *Ann. Rev. Nutr.* 19: 247–277.
- Nagy, K. A., Siegfried, W. R. and Wilson, R. P. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. – *Ecology* 65: 1648–1655.
- Ortiz, C. L., Costa, D. P. and Le Boeuf, B. J. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. – *Physiol. Zool.* 51: 166–178.
- Pennycuik, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. – *Phil. Trans. R. Soc. Lond. B* 300: 75–106.
- Pettit, T. N., Nagy, K. A., Ellis, H. I. and Whittow, G. C. 1988. Incubation energetics of the Laysan albatross. – *Oecologia* 74: 546–550.
- Pinaud, D. and Weimerskirch, H. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. – *Oikos* 99: 141–150.
- Prince, P. A. and Morgan, R. A. 1987. Diet and feeding ecology of Procellariiformes. – In: Croxall, J. P. (ed.). *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge, pp. 135–171.
- Reid, K., Croxall, J. P. and Prince, P. A. 1996. The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at South Georgia. – *Polar Biol.* 16: 469–477.
- Ricklefs, R. E. 1983. Some considerations of the reproductive energetics of pelagic seabirds. – In: Schreiber, R. W. (ed.). *Tropical Seabird Biology*. Allen Press, Inc, Lawrence, pp. 83–94.
- Ricklefs, R. E. 1990. Seabird life histories and the marine environment: some speculations. – *Col. Waterbirds* 13: 1–6.
- Schmidt-Nielsen, K. 1990. *Animal Physiology: Adaptation and Environment*, 4th ed. – Cambridge University Press, Cambridge.
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. 2001a. Behavioural factors affecting foraging effort of breeding wandering albatrosses. – *J. Anim. Ecol.* 70: 864–874.
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. 2001b. Comparison of methods to evaluate energy expenditure of incubating wandering albatrosses. – *Physiol. Biochem. Zool.* 74: 823–831.
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. 2003. Foraging effort in relation to the constraints on reproduction in free-ranging albatrosses. – *Funct. Ecol.* 17: 66–74.
- Speakman, J. R. 1997. Doubly labeled water: theory and practice. – Chapman & Hall, London.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford University Press, Oxford.
- Thomson, D. L., Monaghan, P. and Furness, R. W. 1998. The demands of incubation and avian clutch size. – *Biol. Rev.* 73: 293–304.
- Tickell, W. L. N. 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. – *Ant. Res. Ser.* 12: 1–55.
- Tickell, W. L. N. and Pinder, R. 1975. Breeding biology of the black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. – *Ibis* 117: 432–451.
- Tinbergen, J. M. and Williams, J. B. 2002. Energetics of Incubation. – In: Deeming, D. C. (ed.). *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford University Press, Oxford, pp. 299–313.
- Ward, S., Bishop, C. M., Woakes, A. J. and Butler, P. J. 2002. Heart rate and the rate of oxygen consumption of flying and walking barnacle geese (*Branta leucopsis*) and bar-headed geese (*Anser indicus*). – *J. Exp. Biol.* 205: 3347–3356.
- Warham, J. 1990. *The Petrels: their ecology and breeding systems*. – Academic Press, San Diego.
- Weimerskirch, H. and Guionnet, T. 2002. Comparative activity pattern during foraging of four albatross species. – *Ibis* 144: 40–50.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. P. 2000. Fast and fuel-efficient? Optimal use of wind by flying albatrosses. – *Proc R. Soc. Lond. B* 267: 1869–1874.
- Weimerskirch, H., Mougey, T. and Hindermeier, X. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. – *Behav. Ecol.* 8: 635–643.
- Williams, J. B. 1996. Energetics of avian incubation. – In: Carey, C. (ed.). *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York, pp. 375–416.

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